Taxonomic status of the Gulf Grunion *(Leuresthes sardina)* and its relationship to the California Grunion *(L. tenuis)*

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ABSTRACT.—Statistical comparisons of morphometric and meristic characteristics of the grunions *Leuresthes sardina* and *L. tenuis* support their present status as distinct species. Similarities in fin-ray formulae, gill-raker counts, body proportions and especially reproductive habits justify their placement in *Leuresthes.* The only significant meristic difference between the two is the larger and fewer scales of *L. sardina* (typically 55 lateral scale rows as compared to 75 for *L. tenuis*). Morphologically, *L. sardina* is a longer, more slender fish with shorter pectoral fins and longer pelvic fins than *L. tenuis.* The two species are allopatric: *L. sardina* ranges in the northern Gulf of California from Bahía Concepción, Baja California Sur, and Guaymas, Sonora to the mouth of the Río Colorado; *L. tenuis* ranges from Monterey Bay, California to Bahía Magdalena, Baja California Sur. Their distributions seem to be restricted more by availability of adequate spawning beaches than by sea temperatures.

The Gulf of California grunion, *Leuresthes sardina* (Jenkins and Evermann 1888), and the well-known California grunion, *L. tenuis* (Ayres 1860), are the only two species of fishes known to leave the water and deposit their eggs in beach sand (Figs. 1, 2; Thompson 1919; Walker 1952). Both spawn on a descending series of high spring tides following new and full moons. Their fortnightly spawning runs can be predicted with reasonable accuracy by noting the times of the full and new moon in relation to the height of the high tide (Walker 1952; Thomson 1972). The species are allopatric. *Leuresthes sardina* is endemic to the upper Gulf of California, from Bahía Concepción, Baja California Sur and Guaymas, Sonora to the Río Colorado Delta (Fig. 3). *Leuresthes tenuis* ranges from Monterey Bay, California to Bahía Magdelena on the outer coast of Baja California Sur.

No critical taxonomic comparisons have validated the congeneric status of *L. sardina* and *L. tenuis,* nor fully documented their specific distinction. The forms differ in scale row numbers, body shape and in spawning behavior, as recently noted by Thomson and Muench (1974). The purpose of this study is to statistically compare the morphometric and meristic characteristics of each species, to clarify their taxonomic status, and to elucidate their phyletic relationships.

Taxonomy.—The California grunion was described as *Atherinopsis tenuis* from a specimen taken from a San Francisco fish market by Ayres (1860), and was made the type of a separate genus, *Leuresthes,* by Jordan and Gilbert (1880). In 1896, Jordan and Evermann described a second species in the genus, *L. crameri,* from "Ballenas Bay, Lower California, near Cape Abreojos," and distinguished it from *L. tenuis* on the basis of having fewer lateral scale rows (67 versus 75) and a narrower silvery lateral band. Schultz (1948), however, concluded that *Leuresthes tenuis* and *L. crameri* are conspecific, presumably discounting the lower scale count reported for *L. crameri.*

Taxonomy of the Gulf of California grunion, *Leuresthes sardina,* has been more confused than that of *L. tenuis.* This species was described as *Atherina sardina* by Jenkins and Evermann (1888). *Menidia clara* (Evermann and Jenkins 1891) was synonymized with *A. sardina* by Schultz (1948). Jordan and Evermann (1896) referred *Atherina sardina* to the genus *Menidia* and were the first to suggest

Figure 1. Male Gulf grunion *(L. sardina)* aggregating on the beach at the start of a run at El Golfo de Santa Clara, Sonora, Mexico. (Photo by D. A. Thomson)

a close relationship between *M. clara (=sardina)* and *Leuresthes*, an opinion subsequently supported by Jordan and Hubbs (1919), Breder (1936), Schultz (1948), and Walker (1952, 1960).

Breder (1936) erected a new genus, *Hubbsiella*, for *Menidia clara* on the basis of several characteristics, including that of more lateral scale rows (54-56 as compared with 36-46 in *Menidia*). However, Schultz (1948) stated that the count of 45 lateral scale rows reported by Jenkins and Evermann (1888) for the type of *Atherina sardina* was in error, the actual number being 54. On the basis of similar scale sizes, along with similar structure of gas bladders and vertebral hypophyses, he synonymized *Menidia clara* with *M. sardina*. Schultz accepted the genus, *Hubbsiella*, but noted that *L. tenuis* and *H. sardina* are undoubtedly in the same phyletic line.

Hubbsiella is now generally recognized (e.g. Walker 1960) as being congeneric with *Leuresthes* but the synonymy has not been formally documented.

An otolith from an Eocene deposit at the mouth of the Thames River has been described as *Leuresthes distans* by Stinton (1966), but John E. Fitch and Carl L. Hubbs (pers. comm.) believe this otolith can not be assigned to any living genus, though it is probably from an atherinid. Its reference to a strictly New World genus and subfamily (Atherinopsinae) is highly improbable.

MATERIALS AND METHODS

The specimens of *L. sardina* studied in detail were collected near the head of the Gulf of California at San Felipe in Baja California Norte and at El Golfo

Figure 2. Two Gulf grunion females attended by several males on the beach at El Golfo de Santa Clara. Female in the center of the photo is depositing eggs and males are ejecting milt; female below the center is leaving after spawning. (Photo by D. A. Thomson)

de Santa Clara and Puerto Peñasco in Sonora (Fig. 3). Those of *L. tenuis* were secured in California at Morro Beach, San Luis Obispo, and at Santa Monica, El Segundo, Santa Catalina Island, Cabrillo Beach, Torrey Pines, and La Jolla Shores, in southern California; and from Bahía de Todos Santos, Bahía de Santa Rosalia, and Bahía Magdalena, in Baja California.

Study specimens are housed in fish collections at the University of Arizona (UA), Scripps Institution of Oceanography (SIO), University of California, Los Angeles (UCLA), Los Angeles County Museum of Natural History (LACM), and the California Academy of Sciences (CAS).

Museum catalog numbers, followed by numbers of specimens examined in parentheses, for *L. sardina* are: UA 70-39 (44); UA 70-64-1 (56); UA 72-44-10 (7); UA 73-45 (68); UA 74-9-2 (29); and SIO 65-86 (3). Those for *L. tenuis* are: UA 73-107-1 (42); UA 74-18 (6); UA 74-19-1 (2); SIO H44-40 (19); SIO 74-57 (20); UCLA W51-210 (1); UCLA W49-113 (5); UCLA W49-117 (14); UCLA W55-143 (1); LACM W55-115 (2); LACM 33139-1 (1); LACM 4382 (3); LACM 31306-3 (2); LACM 32597-1 (12); LACM 22307 (2); LACM 31864-12 (2); CAS 25483 (6); CAS 30548 (5); CAS 47320 (1).

Measurements and counts on specimens follow the specifications by Hubbs and Lagler (1947). Body depth was measured vertically above the anus; body width as the distance across the body between the bases of the pectoral fins; and the anal-caudal distance as the length from the anus to the lower mid-line base of the caudal fin. Anal-fin height was measured from the front base of the fin to the tip of its longest front ray.

Figure 3. Geographical distributions of the Gulf of California grùnion, *Leuresthes sardina*, and the California grunion, *L. tenuis*.

Results were analyzed using the student *t*-test and differences are considered to be significant at the 95% probability level. Coefficients of variation were also compared.

RESULTS

Comparison of coefficients of variation show that all meristic counts (V = 0.99 — 9.18) and morphometric measurements (V = 3.56 — 10.75) show average variability (Simpson, *et al.* 1960) except the width of *L. sardina* (V = 14.46). This is probably an artifact of the unavoidable mixing of age classes sampled during

TABLE 1. Means, 95% confidence intervals (CI), samples sizes (N), ranges, and *p*'s of *L. sardina* and *L. tenuis* body measurements expressed as ratios of standard length i.e. SL/measurement. Eye diameter and gill-raker length is reported in proportion to head length.

	L. sardina	*L. tenuis*	
Body measurement	**x̄ ± 95% CI N(Range)**	**x̄ ± 95% CI N(Range)**	***p***
Standard length (mm)	163.5 ± 1.60 207(136-191)	143.8 ± 2.20 145(104-179)	< 0.001
Head length	5.39 ± 0.06 200(6.49-4.68)	5.40 ± 0.45 140(6.67-4.44)	> 0.8
Snout length	17.0 ± 0.21 199(22.3-13.8)	16.6 ± 0.24 144(20.7-13.1)	< 0.01
Eye diameter	4.87 ± 0.16 197(6.70-4.25)	4.10 ± 0.06 150(5.00-3.13)	< 0.001
Bony interorbital width	18.5 ± 0.21 198(23.8-15.1)	18.7 ± 0.23 146(22.8-14.6)	> 0.4
Depth	6.54 ± 0.07 200(8.05-5.08)	6.30 ± 0.07 145(7.14-4.98)	< 0.001
Width	10.8 ± 0.22 145(14.5-8.55)	9.95 ± 0.11 133(11.7-8.41)	< 0.001
Anal-caudal length	2.52 ± 0.04 146(3.11-2.00)	2.36 ± 0.02 108(2.52-2.17)	< 0.001
Gill-raker length	4.59 ± 0.31 30(7.38-4.17)	4.27 ± 0.73 14(5.44-4.00)	> 0.3
Pectoral-fin length	5.99 ± 0.04 200(6.93-5.34)	5.67 ± 0.04 141(6.44-5.14)	< 0.001
Pelvic-fin length	9.65 ± 0.13 198(12.3-8.42)	10.3 ± 0.10 146(11.8-9.21)	< 0.001
Anal-fin height	10.0 ± 0.17 92(12.6-8.06)	11.0 ± 0.23 52(12.5-9.23)	< 0.001

spawning runs. The pelvic and anal spines are always single and the pelvic soft rays always number 5, as in the Atherinidae in general.

All body measurements made, expressed as a ratio of standard length or of head length, are significantly different at the 0.05 probability level except for head length and the bony interorbital width (Table 1). In each species the head length averages 18.5% of standard length, and interorbital widths average 5.4% of the standard length.

Standard length averages about 10 mm longer in *Leuresthes sardina* than *L. tenuis*. Adult females of each species are significantly longer than males, averaging 10 mm longer in *L. sardina* and 13 mm longer in *L. tenuis*. In body depth and body width *L. tenuis* is 4% and 8% the greater, respectively. These differences are significant at $p < 0.001$. *Leuresthes tenuis* is significantly shorter but its anal-caudal length is 4.7% longer ($p < 0.001$). Therefore, the distinctive elongation of the body in *L. sardina* lies between head and anus.

The eye of *L. sardina* is significantly smaller, averaging about 19.6% of head length, as compared to 24.4% in *L. tenuis* ($p < 0.001$). *Leuresthes sardina* has a 2.4% shorter snout than *L. tenuis* thus placing the eye of the Gulf grunion in a slightly more anterior position than that of the California grunion.

Also, there are significant differences in fin lengths. In *L. sardina* the pectoral fins are shorter, and the pelvic fins are longer than those of *L. tenuis* but with overlap in the ratios. Anal-fin height is 9% greater in *L. sardina.*

TABLE 2. Means, 95% confidence intervals (CI), samples sizes (N), ranges, and *p*'s of all counts for *L. sardina* and *L. tenuis*.

Count	*L. sardina* $\bar{x} \pm$ 95% CI N(Range)	*L. tenuis* $\bar{x} \pm$ 95% CI N(Range)	*p*
$Dorsal_1$ spines	5.15 ± 0.14 48(4-6)	5.03 ± 0.14 33(4-6)	>0.2
$Dorsal_2$ soft-rays	9.40 ± 1.39 48(8-10)	9.48 ± 0.31 33(8-10)	>0.9
Anal soft-rays	20.9 ± 0.39 48(19-23)	21.7 ± 0.10 33(19-23)	>0.7
Caudal rays	17.1 ± 0.07 48(17-18)	17.0 ± 0.06 33(17-18)	>0.1
Pectoral rays	13.8 ± 0.17 66(12-15)	13.5 ± 0.27 33(12-15)	>0.05
Gill-rakers	33.4 ± 0.51 48(30-36)	33.7 ± 1.36 33(30-36)	>0.5
Lateral scale rows above lateral band	4.02 ± 0.002 48(4-5)	4.03 ± 0.36 33(4-5)	>0.9
Lateral scale rows below lateral band	5.50 ± 0.12 52(4-7)	7.12 ± 0.19 33(6-8)	<0.001
Lateral scale rows	55.3 ± 0.25 177(51-60)	74.5 ± 0.43 143(69-80)	<0.001

Fin-ray formulae (Table 2) for these species show no statistical difference: D V-I, 9; A I, 20-21; P_1 13-15; as in other atherinids the pelvic-fin rays number I,5 and the principal caudal rays 17 (8 + 9). The first dorsal originates slightly in advance of the anal. The second dorsal is inserted above the middle of the anal fin and the insertion of the last dorsal ray precedes the insertion of the last anal ray. In *L. tenuis* there are 10 to 13 scales between the end of the first dorsal fin and the origin of the second dorsal fin and 8 to 11 interdorsal scales in *L. sardina*. Pelvic fins in each species are inserted far in advance of the first dorsal fin, nearer the tip of the snout than the base of the caudal fin.

Each species has 30 to 36 slender gill rakers on the lower limb of the first gill arch. The longest rakers are about 35% of the head length.

The most diagnostic differences between these two species is in the non-overlapping number of body lateral scale rows. These number 51 to 60 (averaging 55) in *L. sardina*, and 69 to 80 (averaging 75) in *L. tenuis* ($p < 0.001$). Each species has 4 longitudinal scale rows above the lateral band, whereas the number below differs significantly; on the average the Gulf grunion has 6 and the California grunion has 7.

There appears to be no evidence of latitudinal clines within either species in the characteristics discussed above.

Scales also differ conspicuously in shape and size. Although each species has cycloid scales as is usual in the family, those of *L. tenuis* are approximately one-half the anteroposterior dimension and two-thirds the dorsoventral dimension of those of *L. sardina*. Scales on the mid-lateral band of *L. sardina* are entire, with 2 or 3 scallops in the center of the posterior margin, whereas those from the mid-lateral band of *L. tenuis*, are highly and irregularly crenulate. Scales from the last two to three longitudinal rows below the lateral band and above the anal fin in *L. tenuis* are more entire, and similar to those found over the whole body of *L. sardina*. Scales just dorsal to the anal fin in both species are stiffer and tend

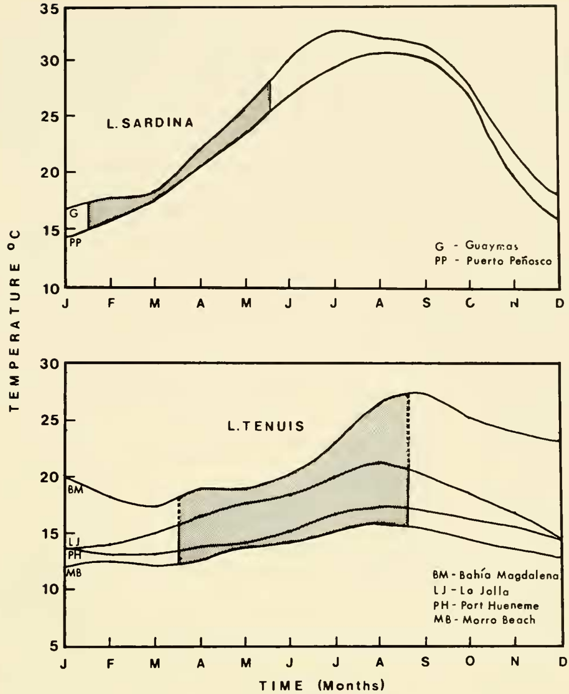

Figure 4. Monthly mean sea-surface temperatures (Robinson 1973; USCGS 1967; and Hendrickson 1974) at several locations in the geographical ranges and the respective spawning seasons (shaded) of *L. sardina* and *L. tenuis*. Sea-surface temperatures at San Felipe and El Golfo de Santa Clara are similar to those at Puerto Peñasco but are not given because long-term temperature records are not available. Dotted lines between temperature curves BM and LJ indicate that frequency of spawning runs have not been established south of Bahía de Todos Santos.

to stand away from the body rather than to lie smoothly as do other body scales. This scale pattern (the "sheath" of Breder 1936, Schultz 1948, and others) is observable in living as well as preserved material, but is less obvious in specimens of *L. tenuis* than those of *L. sardina*. In each species scales extend onto the caudal fin as far posteriad as the first branching of the rays.

Both species have minute and weak recurved teeth, usually in a single row on a strongly downwardly protrusible premaxillary, as described by Jenkins and Evermann (1888) and others. Usually the upper jaw must be dried to see the minute teeth. Teeth of *L. tenuis* are generally weaker and uniserial, and the premaxillary is fleshy. Teeth in *L. sardina* are stronger and sometimes biserial. Occasionally teeth are absent in either species, in which case the jaws are fleshier.

DISCUSSION

Since Jordan and Evermann (1896) first suggested a close phyletic relationship between "*Menidia*" *sardina* of the Gulf of California and *Leuresthes tenuis* of the Californias, some studies have provided supportive evidence, but none have substantiated this relationship by detailed taxonomic analysis. Breder (1936) noted likenesses between the two species in protractile premaxillaries, weak mandibles, general body shapes, short pectoral fins, location of insertion of the first dorsal fins, coloration, and scale sculpturing. Results of the present study show that both species have premaxillaries that can be protruded strongly downward; overall fin insertion is similar; fin-ray formulae do not differ; gill rakers are alike in size and number; and head length and interorbital widths are similar, as is gas bladder and posterior hemal arch morphology (Schultz 1948).

Walker (1960) suggested that the two species are congeneric and he was first to note their "almost identical" beach spawning habit and similar dates of spawning runs (Walker 1952). In view of morphological and behavioral similarities, one might suggest that these fishes represent two allopatic populations of a single species recently isolated, and that any morphological differences between them are clinal ones correlated with past or present environmental gradients; or in light of the description of *L. crameri* (Jordan and Evermann 1896) from Lower California as having a scale count intermediate between *L. sardina* and *L. tenuis* that hybridization has occurred.

None of the differences between *L. sardina* and *L. tenuis* show evidence for latitudinal clines. Nor is there any indication of an intraspecific cline despite the fact that *L. tenuis* specimens were collected from over a 720 mile latitudinal range (Fig. 3). Examination of 26 "*L. tenuis*" specimens from Baja California, 19 of these from Punta Abreojos and Bahía Magdalena, show no significant variation, in any of the characteristics discussed, from *L. tenuis* specimens collected at more northern sites. This supports Schultz's (1948) conclusion (from 2 specimens) that *L. crameri* and *L. tenuis* are conspecific. Gulf grunion populations samples cover too narrow a range to test for clinal variations.

A behavioral difference is also indicated between the two species. *Leuresthes tenuis* is a strictly nocturnal spawner (Walker 1949), whereas *L. sardina* spawns during the day as well as at night. It may be significant that *L. tenuis*, the exclusively nocturnal spawner, has a 20% larger relative eye diameter than *L. sardina*.

Both species spawn over a rather wide range of sea-surface temperatures. *Leuresthes sardina* spawns beginning in late January when monthly mean sea-surface temperatures range from 14° to 17° C throughout its range (Fig. 4). Spawning ceases in May in the northern Gulf when mean sea-surface temperatures range between 23° and 26° C. Throughout the remainder of its geographic range, *L. sardina* is less abundant, and spawning runs are sporadic and not presently predictable.

California and Baja California sea-surface temperatures range from 12° to 16° C when spawning by *L. tenuis* begins in mid-March, from Bahía de Todos Santos to its northern limits. Spawning ceases in this region by mid-August (14° — 19° C). It is not known when spawning begins and ends in the more southern portions of the range of *L. tenuis*, where sea-surface temperatures range from 4° — 11° C higher.

Though little is known of the life history of these two species apart from the spawning behavior, it is believed (Walker 1949) that the California grunion remains in shallow waters not far from spawning beaches. This seems to be the case with *L. sardina* as well. If so, then these fishes are subject to temperatures ranging from 10° to 26° C along the California coasts and from 8° to 31° C in the northern Gulf of California. *Leuresthes sardina* and *L. tenuis* larvae have been shown to have wide temperature tolerance ranges of 7.5° — 32° C (Reynolds, *et* *al.* MS) and with acclimation from 30° to 35° C *L. sardina* tolerates up to 35° C (Reynolds and Thomson 1974).

It seems unlikely that temperature presently limits the distribution of these species in Baja California from Bahía Magdalena southward to Cabo San Lucas and in the Gulf of California as Walker (1960) and Hubbs (1960) suggest, since larvae of these species easily tolerate temperatures occurring in the southern Gulf at Cabo San Lucas. It may be, because of the predilection of young grunion to remain near spawning grounds, that the absence of appropriate spawning beaches in the lower Gulf of California limit the distribution of the grunion in this area.

Hubbs (*in* Breder 1936) suggested that the Gulf grunion ancestral type was probably a form resembling *Hubbesia gilberti.* Schultz (1948) disagreed with this, saying the gas bladders in *Hubbesia* and the other genera retained by him in the subfamily Atherinopsinae, are too dissimilar to postulate *Hubbesia* to be the ancestral type leading to *Leuresthes.* Both Hubbs and Schultz (1948) agree that "*L. sardina* is possibly near the ancestor of *L. tenuis.*" We suggest that *L. sardina* is more primitive than *L. tenuis* because of its stronger dentition and larger scales. Walker (1959) suggested that the grunion's nearest relative is either the California jack smelt *(Atherinopsis californiensis)* or the top smelt *(Atherinops affinis)* both of which, like many members of the Atherinidae, spawn close inshore. Schultz (1948) classified *Atherinops* and *Atherinopsis* in the subfamily Atherinopsinae on the basis of tapering gas bladders somewhat like those in *Leuresthes.* Although none of the Atherinidae possess well-developed lateral-line systems, Freihofer (1972) noted that *L. tenuis* and *Atherinops affinis* have similar distributions of tubed scales.

Hubbs (pers. comm.) supports his earlier suggestion that *L. sardina,* or its ancestor, was ancestral to *L. tenuis,* by pointing out that *L. sardina* more closely resembles the Atherinids as a group than does *L. tenuis,* particularly in view of larger scales and stronger dentition. Hubbs maintains that the finer scales of *L. tenuis,* are typical of the anti-tropical atherinids at terminal evolutionary lines.

The Gulf of California and California grunions have long been recognized to belong to the same phyletic line, the similarities herein described, and particularly their unique spawning behavior justify their congeneric placement. We suggest that major differences here discussed substantiate the specific distinction of *Leuresthes sardina* and *L. tenuis.*

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